SPECIES AND SUBSPECIES

CLASSFICATION, RELATIONSHIPS, LIFE HISTORY, AND EVOLUTION OF *EREBIA MAGDALENA* STRECKER (LEPIDOPTERA: SATYRIDAE)

Gerald J. Hilchie
Department of Entomology
University of Albertan
Edmonto, Alberta T6G 2E3
CANADA

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ABSTRACT

Several populations of Erebia magdalena *Strecker were discovered in Alberta and British Columbia, Canada, all within a limited geographic area. Specimens from the Rocky Mountain states and the sister species* E. mackinleyensis *Gunder from Alaska and Yukon Territory were compared with the newly discovered populations. Principal Component Analysis showed little evidence of introgression of the Alberta populations with populations of* E. mackinleyensis. *Populations of* E. magdalena *from the Rocky Mountain states clustered near and overlapped with the Alberta populations. Discriminant analysis demonstrated a clinal shift in character states within* E. magdalena *which were separate from those of* E. mackinleyensis. *These permitted recognition of different populations. Egg and larval characteristics show similarity between* Erebia magdalena *and* E. mackinleyensis. *Observable differences occur between the* E. magdalena/mackinleyensis *species pair eggs and larvae, and those of* E. fasciata *Butler.* Erebia magdalena saxicola *new subspecies is described. Type locality is Adams Lookout, Wilmore Wilderness Park (43 km southeast of Grande Cache), Alberta.* Erebia magdalena *females oviposit on rocks. Larval development appears univoltine with late instar larvae overwintering. Larvae feed on a variety of grasses.* Erebia magdalena *appears to have evolved from a common ancestor with* E. mackinleyensis *during a pre Wisconsinan glacial period. Subsequent dispersal and isolation resulted in fragmentation and subspeciation. In Alberta* E. magdalena *appears derived from ancestral populations formerly located in the Montana front ranges during the last glacial stage.*

INTRODUCTION

Erebia magdalena Strecker was known to inhabit high mountain boulder fields and talus slopes in alpine scree of northern New Mexico, Colorado, Wyoming, Utah, and southern Montana (Ferris and Brown, 1980). Inaccessibility and remoteness have limited collection of this species in many parts of its range. Its discovery in Alberta and adjacent British Columbia raises some interesting questions. What are the affinities of these populations with other populations of *E. magdalena* and those of its seemingly close relative *E. mackinleyensis* Gunder? Why has this butterfly species not been found in the mountain areas between Wilmore Wilderness Park (near Grande Cache), Alberta and Carbon County, southern Montana? Is it a relic of pre- or post- Wisconsinan dispersal? To attempt to answer these questions, populations of *E. magdalena* are compared with each other and with populations of *E. mackinleyensis*. Aspects of life history are included as further characterization.

MATERIAL AND METHODS

Material

Study material included: 242 adults, eggs, egg shells, larvae, 1 pupa, and photographic material of life stages of *Erebia magdalena*; 54 adults, eggs, egg shells and larvae of *E. mackinleyensis*; and and eggs, egg shells and larvae of *Erebia fasciata*.

The following codens designate collections cited in this paper. Names of curators or owners of private collections are in parentheses following the address of each collection.

ALME	Allyn Museum of Entomology, 3701 Bay Shore Road, Sarasota, Florida 33580. (L.D. Miller).
AMNH	American Museum of Natural History, Central Park West at 79 Street, New York, New York 10024. (F.H. Rindge).
AVER	Avery Collection, Hinton, Alberta. (K. Avery).
CNC	Canadian National Collection, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6. (J.D. Lafontaine).
HILC	Hilchie Collection, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3. (G. J. Hilchie).
INHS	Illinois Natural History Survey, 172 Natural Resources Building, Urbana, Illinois 61800. (K.C. McGiffen).
PIKE	Pike Collection, Department of Biology, University of Calgary, Calgary, Alberta T2N 1N4 (E. M. Pike).
PRES	Preston Collection, Lawrence Kansas. (J. & F. Preston).
SHEP	Shepard Collection, Sproule Cr. Road, Nelson, B.C. (J. Shepard).
SPER	Sperling Collection, Department of Ecology and Systematics, Cornell University, Ithaca, New York, 14853. (F. A. H. Sperling).
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta, T6G 2E3. (D. Shpeley).
USNM	United States National Museum, Smithsonian Institution, Washington, D.C. 20560. (R.K. Robbins).
YOUN	Young Collection, 256 Clear Falls Circle, Eagle River, Alaska 99577. (M. E. Young)

Methods

Several populations of *E. magdalena* were examined critically for similarities and differences to assist in recognizing species and subspecies boundaries. Characters used in the analysis include scale pattern and color, on the wings and antennae, measurements, structure of male genitalia and structure of the egg. Data generated from the study was examined statistically.

Measurements.— Specimens were examined using a Wild M5 microscope equipped with an ocular micrometer. Wing length measurements were made from base to margin at R4 for the forewing and from base to margin at M3 on the hindwing. Larval head capsule widths were measured frontally at the widest point. Egg capsules were measured for length (apex to base) and width (widest point).

Scale pattern and color.— Wing scale and hair counts were made on limited regions of the fore and hindwings. On the forewing the area was delimited by the veins R4 and R5 and the wing margin. On the hindwing the area was delimited by the veins M1 and M2 and the wing margin.

Medial band on the hind wing was indexed as three character states: present and clearly defined; present but faint and indistinctly defined; and absent. The presence and extent of pattern exhibited by rust coloured scales was indexed as five character states (only three listed): no rust scales; a few scattered scales; large well defined patch. Variation of pigmentation of the antennal club was indexed as seven character states dependent on colour and pattern of light and dark areas. Indexing of the antennal club did not use color patterns of the covering scales as these were badly abraded on many specimens. Index values were polarized to reflect recognized taxa, with low numbers assigned to *E. magdalena* and higher numbers to *E. mackinleyensis*

Male genitalia.— Male genitalia were studied by removing the terminal segments of the abdomen and placing them in hot 10% KOH solution until soft. Illustrations were made with the aid of a camera lucida on a Wild M5 microscope. Then genitalia and terminal segments of the abdomen were placed in glycerol in a microvial which was pinned through its cork beneath the specimen of origin.

Egg and larval structures .— Egg and larval structures were examined and photographed with the aid of a Zeiss Tessovar light microscope and Cambridge Stereoscan 250 and 100 Electron Scanning Microscopes.

Chromosome study.— Butterflies were brought to the lab alive, frozen at -20°C and stored until chromosome fixing. Frozen testes were dissected and fixed in 95% ethanol:acetic acid (3:1). Testes were Fuelgen stained, squashed in 50% acetic acid and preserved in Euparol.

Life history study.— Caged females were given substrate choices (rocks, lichens, grasses, willow twigs and leaves) on which to oviposit. Eggs were collected for rearing and taxonomic study. Larvae initially were given a choice of food until the food preference was determined. Larvae were reared to maturity in petri dishes, lined with absorbent toweling, and supplied with fresh leaves daily. Incubators were used to control environmental conditions for part of the rearing.

Statistical analysis.— Data obtained were subjected to Principal Component Analysis, Discriminant Analysis and Cluster Analysis for evaluation of variance and relationship between populations and individuals. Statistical manipulations were made with the Michigan Interactive Data Analysis System (MIDAS) on the Amdhal Computer at the University of Alberta.

The data were pooled to provide population samples of adequate size for statistical analysis. Small samples that could not be pooled were excluded from the initial analysis, then compared with the results on an individual basis.

CHARACTER ANALYSIS

Characters for species and subspecies designation in *Erebia* species are based on structural differences in genitalia, chromosome number, wing venation, wing shape, differences in maculation and scale types (Warren, 1936). Lesser levels of difference in maculation pattern with geographic isolation serve as criteria for subspecies discrimination.

Warren (1936) commented "There is obviously little possibility of showing variation" in reference to the uniform black colour of *E. magdalena*. This results in placing more emphasis on character states which do show variation.

Table 1. Comparison of males of *Erebia mackinleyensis* and *E. magdalena* adult males using measurements and character index values.

Character	Species													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon n=39		Alberta to New Mexico n=167		Alberta n=28		Montana n=6		Utah n=20		Colorado n=95		Colorado (south) & New Mexico n=18	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.7	22.8-28.9	25.1	21.4-28.9	23.8	21.4-26.1	24.9	24.2-25.8	25.7	21.9-27.7	25.3	21.9-28.9	25.1	23.5-27.9
-white scale index	0.33	0-10	1.5	0-26	4.6	0-26	7.2	2-16	3.3	0-24	0.18	0-10	0.33	0-3
-white hair index	3.2	0-38	2.1	0-35	1.7	0-10	10.5	2-22	5.5	5.5-35	1.1	0-20	1.8	0-14
Hindwing														
-length (mm)	21.5	18.2-23.8	20.9	17.7-23.5	19.9	17.7-21.7	20.7	19.8-21.4	21.2	18.2-23.3	21.1	18.2-23.5	20.8	19.1-22.6
-white scale index	0.03	0-1	3.6	0-48	8.7	0-48	13.5	0-38	1.5	0-12	1.8	0-32	3.9	0-42
-white hair index	1.3	0-28	1.7	0-46	1.0	1-10	11.0	0-33	0.35	0-5	1.2	0-27	4.2	0-46
Wing markings														
-mesial band index	2.5	1-3	1.7	1-3	1	1	1	1	1	1	1.1	1-3	1.2	1-2
-dorsal rust patch	1.7	1-5	1	1	1	1	1	1	1	1	1	1	1	1
-ventral rust patch	3.2	1-6	1.02	1-3	1	1	1.5	1-3	1	1	1	1	1	1
Antennal club														
-color index	3.6	1-8	5.9	4-8	6.4	5-7	7.0	5-8	6.4	4-8	5.6	5-8	6.1	5-8

Table 2. Comparison of *Erebia mackinleyensis* and *E. magdalena* adult females using measurements and character index values.

Character	Species													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon n=15		Alberta to New Mexico n=75		Alberta n=20		Montana n=3		Utah n=4		Colorado n=42		Colorado (south) & New Mexico n=6	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.8	23.5-28.2	25.3	22.1-28.0	25.0	22.1-27.7	25.5	24.9-26.3	25.4	23.7-26.3	25.3	22.4-28.0	26.5	24.5-27.5
-white scale index	4.9	0-39	20.6	0-200	46.4	3-200	49.3	21-105	6.7	4-13	9.7	0-30	5.5	0-14
-white hair index	18.8	0-52	68.5	1-218	66.5	2-150	84	49-137	33	17-68	74.9	1-218	46	0-111
Hindwing														
-length (mm)	21.5	19.1-22.8	21.0	17.2-23.3	20.5	17.2-22.8	21.4	19.8-22.6	20.8	19.8-21.4	21.1	18.2-23.3	21.9	20.0-23.3
-white scale index	3.9	0-23	31.8	0-135	59.6	6-135	53.7	25-97	6.0	0-14	17.9	0-93	41.8	0-97
-white hair index	4.5	0-24	73.5	0-258	51.8	0-153	168.3	139-216	9.7	1-29	8.5	0-258	63.8	0-147
Wing markings														
-mesial band index	2.9	2-3	1.8	1-3	1	1	1	1	1	1	2.4	1-3	2	2
-dorsal rust patch	5.4	1-6	1.2	1-6	1.05	1-2	4	3-6	1.25	1-2	1.09	1-5	1	1
-ventral rust patch	5.0	1-6	1.1	1-5	1	1	1.7	1-3	1.25	1-2	1.09	1-5	1	1
Antennal club														
-color index	2.7	2-4	6.1	5-8	6.8	6-8	6.0	5-8	7	7	5.7	5-7	6.0	5-7

External Features

Erebia magdalena is one of the plainest butterfly species in North America, with adults uniformly black to dark brown. Other colours and patterns are absent from most specimens. Data on populations sampled are presented in Tables 1 and 2. Few females have a reddish flush (6.7%, n=75), with one population (Montana, Beartooth Plateau) in which all females examined (n=3) and one of the males (n=5) were marked. Ventral maculations are slightly developed to obsolete with considerable variation between localities. Most females from Colorado (80%, n=45) are banded (Figure 43) while females from Alberta, Montana, Utah, New Mexico (n=20, 3, 4, 4) were unbanded. Most males lack ventral banding. Degree of coverage by scattered white hairs and scales on the ventral wing surface varies markedly. When present in quantity the white scales and hairs dusted the ventral apex of the forewing and were more evenly distributed on the hind wing. In females from Colorado these scales enhance the banding pattern on the hind wing but do not do so on females from Alberta. Markings on the antennal club vary, but on average it has a dark piceous half partially bisected by a longitudinal strip lighter in colour. The remaining half of the club is paler on many adults. Scales obscure the boundaries of the markings (Figure 41).

Data for the Principal Component Analysis were placed in the following groups for comparative purposes (males, females):

E. magdalena

CANADA. Alberta, (Mount Hamell 11, 4; Adams Look Out 17, 15; Dore River, B.C. 0, 1). U.S.A. Montana (Beartooth Plateau of Montana and Wyoming 6, 3). Utah (Summit, Duchesne and Uintah Counties 20, 4). Colorado, northern (Larimer, Grand, Gilpin and Boulder Counties 42, 18). Loveland Pass, (central Colorado 40, 13). Colorado, southern (Gunnison, Park, Hinsdale, La Plata, Custer, *etc*. Counties 27, 14). New Mexico (Taos County 4, 3).

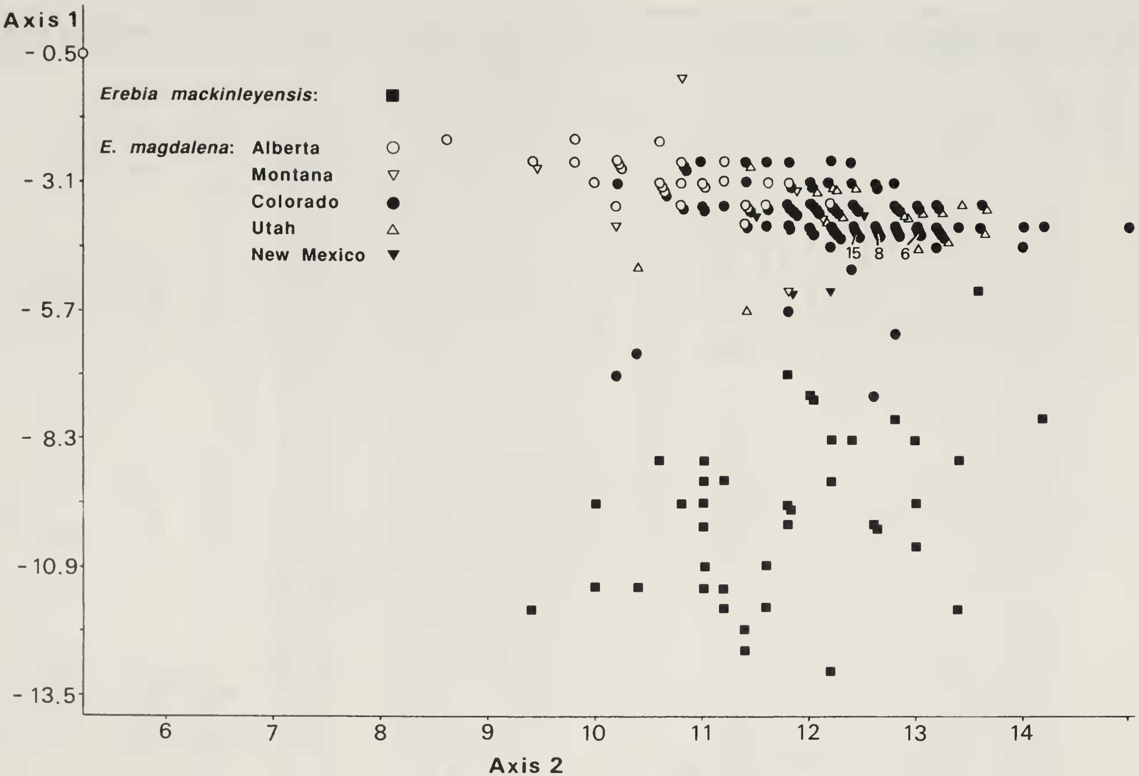
E. mackinleyensis

CANADA. Yukon (Dempster Highway 37, 11). U.S.A. Alaska (2, 4)

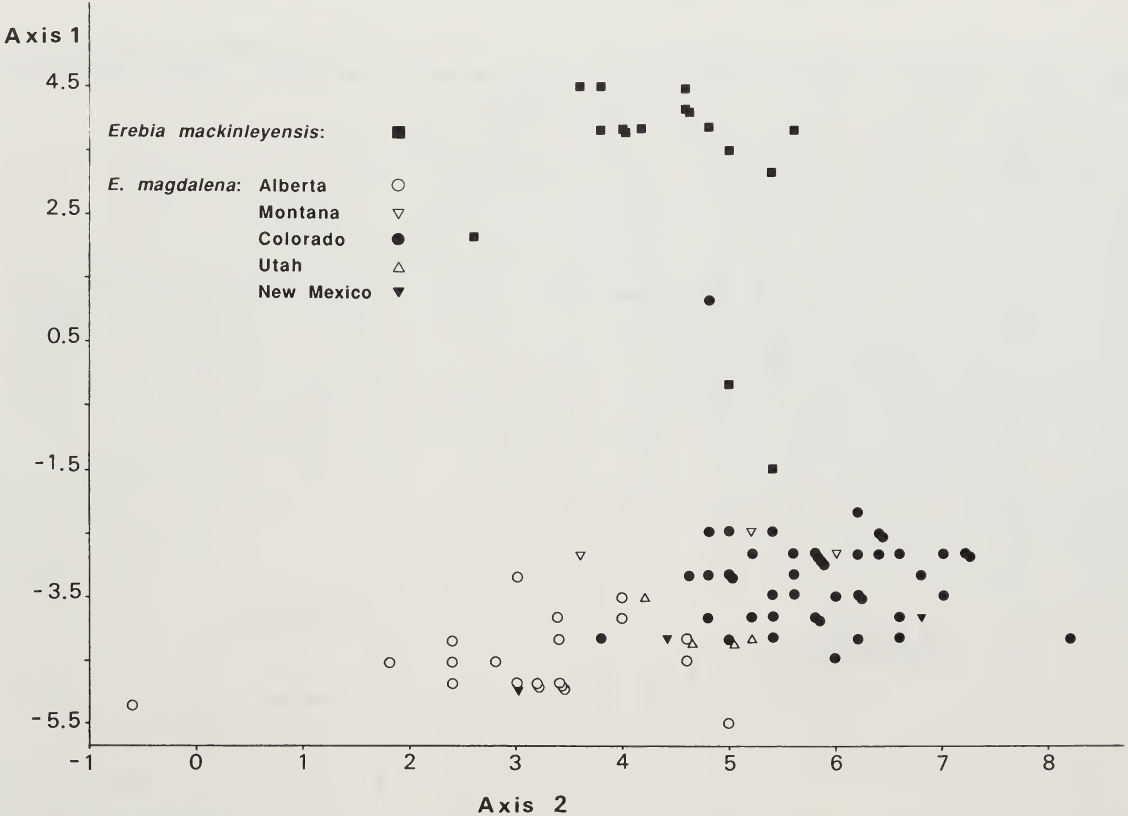
Results from Principal Component Analysis of the various populations support the idea that *E. magdalena* and *E. mackinleyensis* are separate and recognizable entities as shown in Graphs A and B. Tables 1 and 2 list the mean values for variables used in the analysis and their range of variation expressed by length, or indexed value. Populations of *E. magdalena* show a trend (Graphs A and B: Tables 1 and 2): data points cluster but are skewed geographically. Northern (Alberta) specimens appear as one end of a cline, with intermediate individuals forming a blend zone with southern (Colorado) specimens. Albeit the Montana sample is small, the specimens examined tend to be somewhat intermediate in placement, along with specimens from Utah. It is clear that these populations belong together; it is also clear that there are recognizable differences between the populations. Discriminant Analysis and Cluster Analysis exhibited similar results.

Male Genitalia

Males of *E. magdalena* (Figures 31–36) are very similar in genitalic structure to males of *E. mackinleyensis* (Figures 37 and 38). Spination of the claspers (Figures 32b-36b) is along the outer margin. In males of *E. mackinleyensis* (Figures 37b-38b) the spines are expanded onto the inner face. Warren (1981) reports the dorsal parts of the uncus and brachia are on a smaller



Graph A. Principal Component Analysis of adult females of *Erebia mackinleyensis* and several populations of *E. magdalena* from Alberta, Montana, Colorado, Utah and New Mexico. (Re-plotted from computer printout.)



Graph B. Principal Component Analysis of adult males of *Erebia mackinleyensis* and several populations of *E. magdalena* from Alberta, Montana, Colorado, Utah and New Mexico. (Re-plotted from computer printout.) Numbers refer to numbers of individuals whose scores fall on one plotting point.

scale in *E. mackinleyensis*. Variation in shape and size of parts of the male genitalia of *E. magdalena* as shown in Figures 32–36 (male claspers) indicate that size and shape do not discriminate these species reliably.

Conclusions

Erebia mackinleyensis and *E. magdalena* have been considered as conspecfic subspecies (*e.g.*, Ehrlich and Ehrlich 1961, Howe 1975). The distinct appearance of the adults, structural differences in male genitalia and vicariance strongly suggest separate gene poois. Until genetic compatibility is determined, I accept Warren's (1981) decision in recognition of *Erebia magdalena* and *Erebia mackinleyensis* as distinct species. Further I suggest that they are sister species.

Based on phenetic differences and geographical disjunction, the populations of *Erebia magdalena* form two identifiable groups. These groups deserve subspecific recognition, with the names that are given them serving as convenient designations for use by systematists and others. Although some individuals reject the formal recognition of a subspecies category, I accept the position taken by Willis (1967): "... if a subspecies reflects to some degree the actual pattern of variation, as well as being convenient 'handles' for reference, their value seems sufficient to justify their recognition".

TAXONOMIC TREATMENT

Erebia magdalena Species Group

Similarities in structure of the male genitalia place *Erebia magdalena* and *E. mackinleyensis* in a group with *E. fasciata* Butler, *E. semo* Grüm-Grschimailo and *E. erinnyn* Warren (Warren 1936,1981). The *magdalena* group is subdivided on the presence or absence of male androconial scales. *Erebia magdalena*, *mackinleyensis*, *semo* and *erinnyn* are included in the subgroup which possesses androconia (*erinnyn* is assumed by Warren to have androconia). Reduction of the

Table 3. Comparison of larval head capsule width, and egg diameter and length for *Erebia magdalena, E. mackinleyensis* and *E. fasciata*.

Stadia	Species							
	E. m. mag.		*E. m. sax.*		*E. mack.*		*E. fasc.*	
Egg dia.	1.23		1.22±0.07		1.10±0.09		1.03±0.05	
lgth.	1.36	n=3	1.45±0.07	n=25	1.28±0.05	n=11	1.27±0.08	n=11
Instar								
1st	0.74	n=3	0.81±0.02	n=25	0.74±0.03	n=13	0.69±0.03	n=12
2nd			1.18±0.04	n= 4	1.05±0.04	n=19	0.99±0.04	n=16
3rd			1.55±0.02	n= 5	1.51±0.07	n=19	1.41±0.05	n=36
4th	2.15	n=2	2.19±0.04	n=10	2.13	n= 3	2.00±0.06	n= 5
5th	3.15	n=2	3.00±0.10	n=10	3.00	n= 1	2.79	n= 3

Units are in mm, error limit is ± one standard deviation Abbreviations used: diam. = diameter; *E. m. mag.* = *E. m. magdalena; E. m. sax* = *E. m. saxicola; E. m. mack.* = *E. mackinleyensis; E. fasc.* = *E. fasciata.*

mesal banding pattern helps to unify the subgroup. The uniform black color of *E. magdalena* in both sexes differentiates the species from *E. mackinleyensis* and *E. erinnyn*. *Erebia erinnyn* is Asian while *E. mackinleyensis* is North American.

Erebia fasciata Butler 1868
(Figures 51 and 52, Table 3)

Eggs and larvae were examined and compared with immatures of *Erebia mackinleyensis* and *E. magdalena* .

Material Examined.—

Immatures. CANADA. Yukon; Dempster Highway, 14 eggs and egg shells, 11 first larvae, 4 second instar larvae, 38 third instar larvae, 4 fourth instar larvae, 3 fifth instar larvae and associated exuviae (HILC).

Erebia mackinleyensis Gunder 1932
Figures 37, 38, 40 and 44 - 50, Tables 1, 2 and 3)

Recognition.— Most adults are easily recognized by reddish wing patches to well marked bands on the wings. Geographic locality in Alaska and Yukon Territory further assists in identification.

Description.—

Adults (Figures 37, 38, 40 and 44). Form, shape and general appearance are similar to *E. magdalena* as mentioned by Gunder's original description (1932). Data are summarized in Tables 1 and 2. Maculations are more prevalent in both sexes. Most females (91%, n=15) display a conspicuous rust patch on the forewing (Figure 44) or at least scattered rust scales. Males show the same marking but at a lower frequency (74% n=39). Both sexes have a ventral mesial band on the hind wing (males 97%, n=39; females 100%, n=15). Few white hairs and scales are present on either sex. The antennal club is different from *E. magdalena* in that it tends to be testaceous to two-toned yellow (Figure 40). A few *E. mackinleyensis* adults had darker antennal clubs (7.5%, n= 39 males, 0%, n=15 females) resembling those of *E. magdalena*.

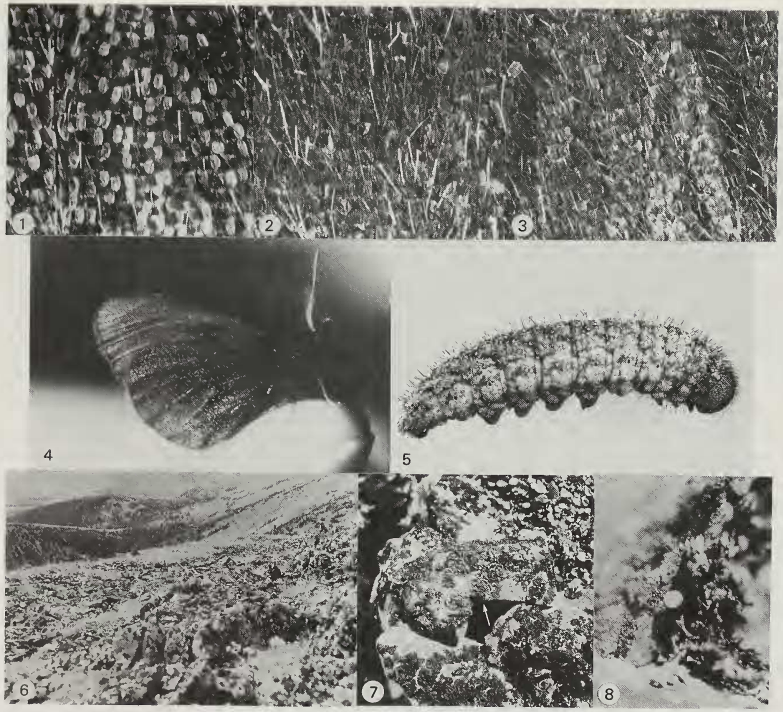
Male genitalia are similar to those of *E. magdalena* The spination on the uncus is expanded onto the inner surface (Figures 37 and 38).

Larvae (Figures 46–50, Table 3). Larvae were indistinguishable from those of *E. magdalena* but differed from those of *E. fasciata*. *Erebia fasciata* larvae were similar in body appearance structurally but differed in maculation pattern and first instar larvae (Figure 52) showed differences in the sculpture pattern of the head capsule. Measurements of head capsule are summarized in Table 3.

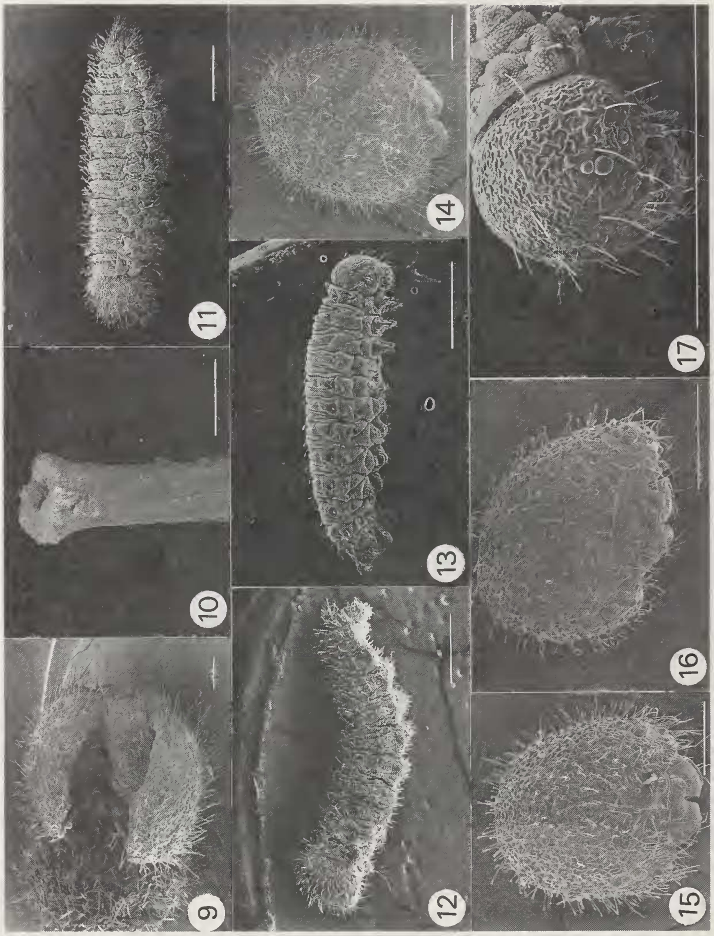
Egg (Figure 45). Sculpture and shape are very similar to that seen in eggs of *E. magdalena*, length 1.10 mm, diameter 1.28 mm, (n= 11). The area around the micropyle appears different; (compare Figures 24 and 45). The basic ground plan pattern is similar but differs in the number of micropyle holes (the differences could be due to individual variation). For comparative purposes the micropyle region of a third species of the *magdalena* group was examined, *E. fasciata* (Figure 51). On the eggs of this species the micropyle region is very similar to that seen on the eggs of *E. mackinleyensis* with only slight symmetry differences of the openings.

Geographical Distribution.— *Erebia mackinleyensis* is known from alpine tundra rock pile habitat in Alaska and Yukon Territory. The southern range limits in the mountain regions have not been documented.

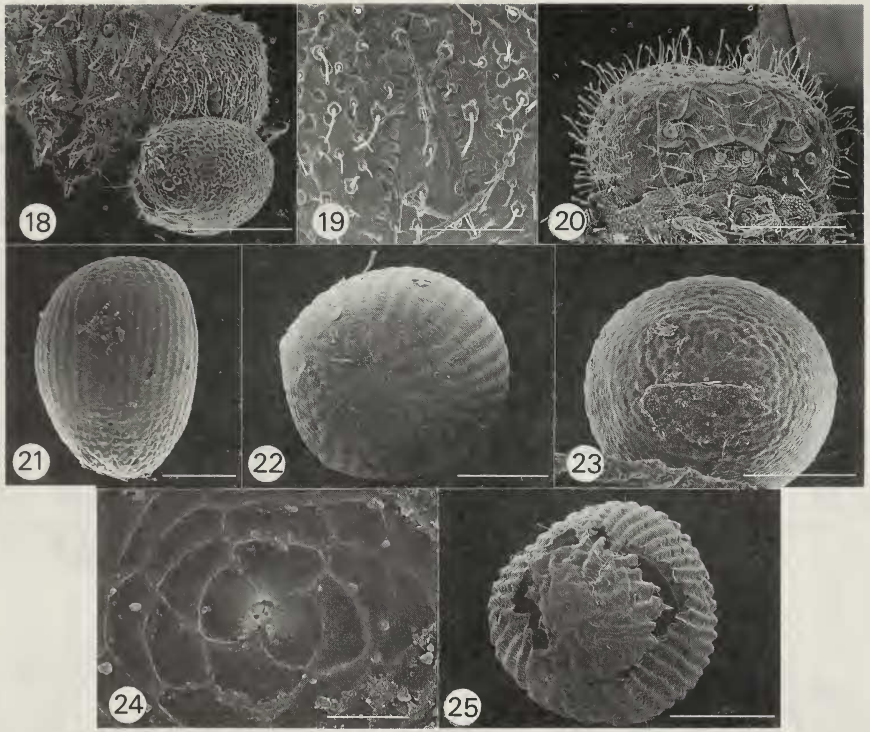
Chorological Affinities.— *Erebia mackinleyensis* occurs in areas inhabitated by other species of *Erebia*. *Erebia fasciata* is often found in close proximity. Ferris *et. al.* (1983) report on the occurrence of *E. erinnyn* in North America but the butterfly prefers low elevation moist meadow habitat and thus is not in contact with populations of, *E. magdalena* .



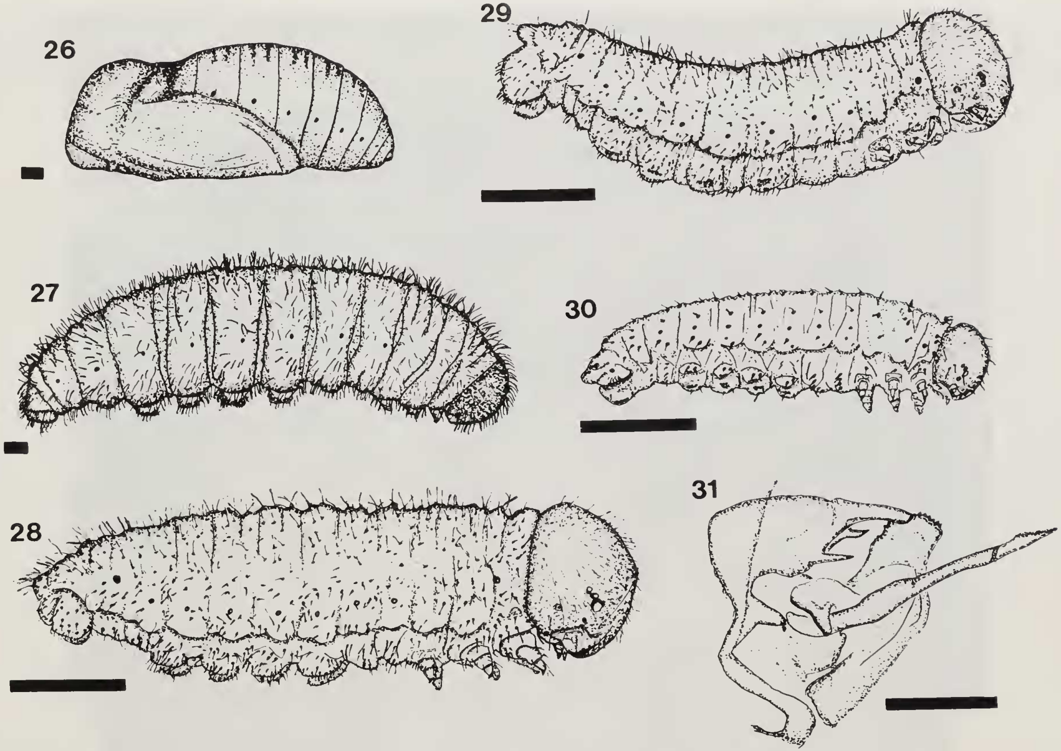
Figures 1-8. Fig. 1. White scales and hairs on ventral forewing surface of *E. magdalena saxicola* female. Fig. 2. White hairs on ventral hindwing surface of *E. m. saxicola* male. Fig. 3. Dark scales and hairs on ventral forewing surface of *E. m. magdalena* female. Fig. 4. Adult female of *E. m. saxicola*; note dusting of white on the wings. Fig. 5. Fifth instar larvae of *E. m. saxicola*. Fig. 6. View of type locality, Adams Lookout, Wilmore Wilderness Park, boulder field near top of mountain, interspersed with patches of vegetation. Fig. 7. Natural oviposition side, egg deposited under edge of rock near arrow. Fig. 8. Egg on underside of rock in Fig. 7.



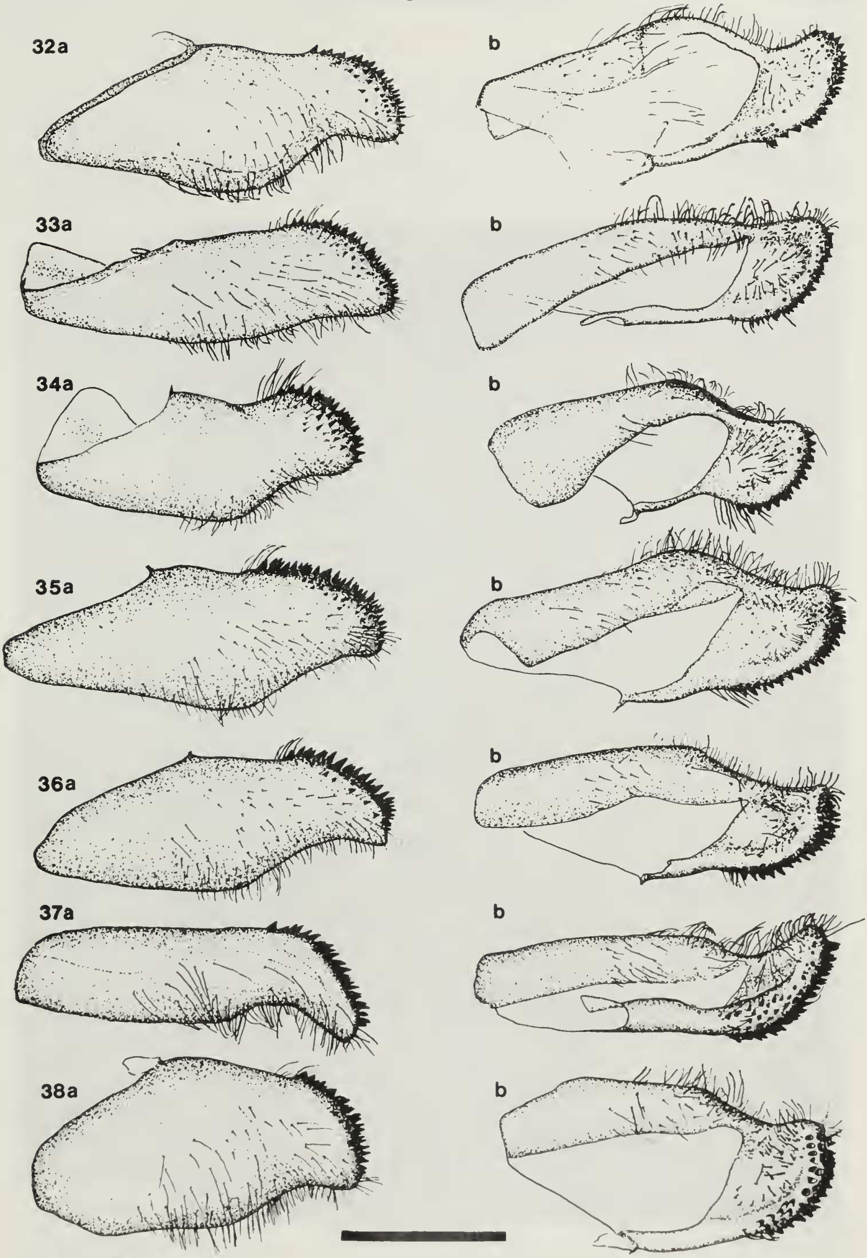
Figures 9-17. Scanning electron micrographs of *E. magdalena saxicola*. Scale line = 1 mm unless specified otherwise. Fig. 9. Cast cuticle from fifth instar larva. Fig. 10. Tip of fifth instar larval body hair; scale = 50 mm Fig. 11. Third instar larva. Fig. 12. Second instar larva. Fig. 13. First instar larva. Fig. 14. Fourth larval instar head capsule. Fig. 15. Third larval instar head capsule. Fig. 16. Second larval instar head capsule. Fig. 17. First larval instar head capsule.



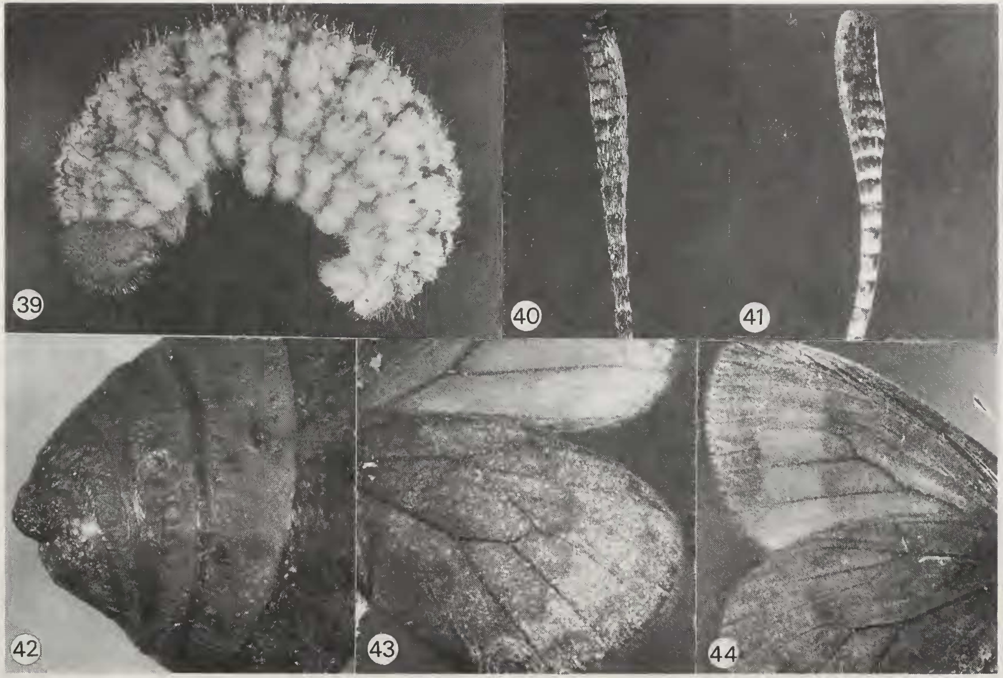
Figures 18-25. Scanning electron micrographs of *E. magdalena saxicola*. Scale line = 0.5 mm unless specified otherwise. Fig. 18. First instar molting to second instar larva. Fig. 19. Sutures on head of third instar larva. Fig. 20. Mouthparts of third instar larva. Fig. 21. Lateral view of egg. Fig. 22. Apical view of egg. Fig. 23. Basal portion of egg: note patch of adhesive material. Fig. 24. Micropyle on apex of egg; scale = 20 mm. Fig. 25. Egg after emergence of larva.



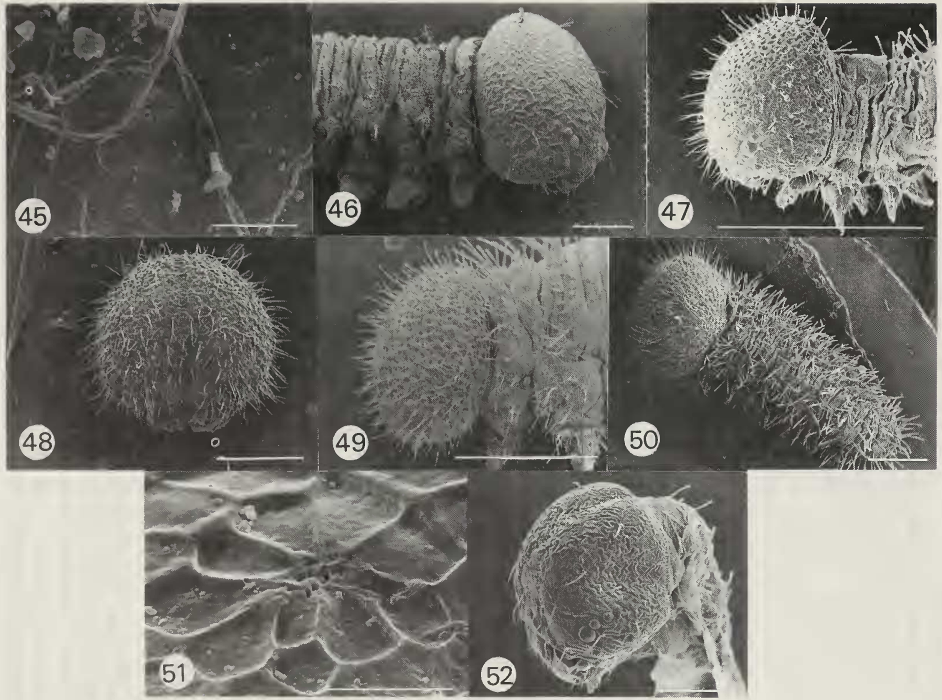
Figures 26-31. Line drawings of *E. magdalena saxicola*. Scale line = 1 mm. Fig. 26. Pupa. Fig. 27. Fifth instar larva. Fig. 28. Third instar larva. Fig. 29. Second instar larva. Fig. 30. First instar larva. Fig. 31. Male genitalia with left clasper removed.



Figures 32-38. Line drawings of the left clasper of male genitalia for *E. magdalena magdalena*, *E. m. saxicola* and *E. mackinleyensis*. Drawing **a**, view of outer surface, dorsal to the top of the page; drawing **b**, inner surface, dorsal side to bottom of page. Scale line = 1 mm. Fig. 32 *E. m. saxicola*, Adams Lookout. Fig. 33. *E. m. saxicola*, Adams Lookout. Fig. 34 *E. m. magdalena*, Utah. Fig. 35. *E. m. magdalena*, Maroon Pass, Colorado. Fig. 36. *E. m. magdalena*, Mount Audubon, Colorado. Fig. 37. *E. mackinleyensis*, Dempster Highway, km 131, Yukon. Fig. 38. *E. mackinleyensis*, Dempster Highway, Km 468, North West Territories.



Figures 39-44. Photographs of *E. magdalena magdalena*, *E. m. saxicola* and *E. mackinleyensis*. Fig. 39. Fifth instar larva of *E. m. magdalena*, reared from eggs collected at Wheeler Basin, Colorado by M. E. Young, 1973. Fig. 40. Left antennal club of *E. mackinleyensis*, *Dempster Highway, Yukon*. Fig. 41. Left antennal club of *E. m. saxicola* Adams Lookout, Alberta. Fig. 42. Abdomen of pupa of *E. m. saxicola*, reared from eggs from females collected at Adams Lookout, Alberta (adult emerged 1983, see Fig. 4.). Fig. 43. Ventral hind wing of female *E. m. magdalena*, showing enhanced banding pattern with white scales, Mount Kelso, Colorado. Fig. 44. Ventral forewing of female *E. mackinleyensis* with distinct rust patch, Dempster Highway, km 465, Yukon.



Figures 45-52. Eggs and reared larvae of *E. mackinleyensis* and *E. fasciata*. Eggs were collected by P. Ross from captive females, 1985, Dempster Highway, Yukon. Fig. 45. Egg micropyle of *E. mackinleyensis*. Scale line = 20 mm. Fig. 46. First instar larva of *E. mackinleyensis*. Scale line = 0.2 mm. Fig. 47. Second instar larva of *E. mackinleyensis*. Scale line = 1 mm. Fig. 48. Larval head capsule of third instar larva of *E. mackinleyensis*. Scale line = 1 mm. Fig. 49. Lateral view of third instar larvae of *E. mackinleyensis*. Scale line = 1 mm. Fig. 50. Dorsal view of third instar larvae of E. mackinleyensis. Fig. 51. Micropyle region on egg of *E. fasciata* Scale line = 20 µm. Fig. 52. Head of first instar of *E. fasciata*. 0.2 mm.

Phylogenetic Relationships.— The *E. magdalena /mackinleyensis* species pair exhibits many characters which unite them as sister species: structure of male genitalia; lack of maculations from most adults; when maculations are present, a similarity of design; and presence of andriconial scales in the males. Other related species are *E. erinnyn* (Siberia, except for the presumed Canadian record); and *E. fasciata.*

Material Examined.—

Adults (males, females). CANADA: Yukon; Dempster Highway, Km 154 to 156, 34, 10 (CNC, HILC, PIKE, PRES, SHEP, SPER). Dempster Highway, Km 465 to 468, 3, 1 (CNC). U.S.A.: Alaska; Atigun Gorge, north ridge, 2, 4 (SHEP).

Immatures. CANADA: Yukon; Dempster Highway, Eggs 20 eggs and egg shells, 17 first instar larvae,16 second instar larvae, 12 third instar larvae, 2 fourth instar larvae, 1 fifth instar larvae and associated exuviae (HILC).

Erebia magdalena Strecker 1880
(Figures 1 – 5, 8 – 36, 39 and 41 – 43, Tables 1 – 3)

Recognition.— This is perhaps the plainest butterfly species in North America, most specimens exhibiting a uniform dull black to dark brown color.

Description.—

Adults (Figures 1–4, 31–36, and 41). Wings dark blackish brown, population variations occur with some individuals exhibiting banding ventrally, and others developing a rust colored patch. See the discussion on character states under Character Analysis. Body similar color to the wings. Antennae annulated with gray white, club ferruginous above, black below (Figure 41).

Male genitalia as illustrated (Figures 31–36). Spination of uncus not expanded to inner surface as in *E. mackinleyensis* (Figures 37 and 38). Chromosome numbers reported by Maeki and Remington (1960) for *E. magdalena* from Gunnison County, Colorado were 10 large, 11 medium and 8 small for a sum of 29.

Immatures (Figures 5, 9–28, 39, 42; Table 3). Pupa (Figures 26 and 42). Alberta specimen (n=1); Length, 14 mm long. Head and thorax regions olive to dark green with abdomen medium brown tinged with green, without distinct markings, spines or hairs. Cremaster blunt, rounded (Figure 42), sculpturing on abdominal sclerites is a series of short longitudinal lines (Figure 42). Silk not observed. Colorado specimen; (from photo, YOUN) similar to Alberta specimen.

Larva, fifth instar (Figures 5 and 27). Alberta specimens (n=10); Integument with numerous blunt hairs (Figure 10). Head capsule dark brown, ground color of body green with black mottled maculations (Figure 5). Head capsule width 3.00 ± 0.10 mm. Colorado specimens (n=2); head capsule lighter brown, photo of larvae show light green ground colour, head capsule width 3.15 mm.

Larva, fourth instar. Alberta (n=10); Similar to fifth instars except smaller and with fewer hairs. Head capsule (Figure 14), width 2.19 ± 0.04 mm, n= 10. Colorado specimens (n=2); Ground colour cream in preserved specimens, head capsule width 2.15 mm.

Larva, third instar (Figures 11 and 28). Alberta specimens (n=5); similar to fourth instars, with reduced maculation and fewer hairs. Head capsule (Figure 15) width 1.55 ± 0.02 mm. Colorado specimens not seen.

Larva, second instar (Figures 12 and 29). Alberta specimens (n=4); hairs very few, no obvious maculations, ground color green. Head capsule, brown, lightly rugose (Figure 16) width 1.18 ± 0.04 mm. Colorado specimens not seen.

Larva, first instar (Figures 13 and 30). Alberta specimens (n=25); hairs very few, in discrete pattern. Ground color various from cream to light green with no dark maculations. Head capsule (Figure 17) with markedly rugose sculpture. Head width measurements 0.812 ± 0.018 mm. Colorado specimens (n=2); Similar ground colour, cream in preserved specimens, head capsule width 0.743 mm. Published illustration in Edwards [1888, collected by Mr. Bruce at Hall Valley, Mount Bullion (Edwards 1951)].

Egg (Figures 8, 21–25). Alberta specimens (n=25); ovoid with rounded ridges on sides (Figure 21). Top and bottom with rounded bumps (Figures 22 and 23). Micropile centered at apex (Figure 24). Color cream, darkened just before hatching. Length 1.45 ± 0.07 mm with diameter of 1.22 ± 0.07 mm. Bottom glued to substrate during oviposition (adhesive pad on bottom of egg, Figure 23). Colorado specimens (n=3); Similar in appearance, length 1.36 mm, diameter 1.23 mm. Published illustration in Edwards (1888).

Geographical Distribution.— *Erebia magdalena* is known from the high alpine meadows of northern New Mexico, through Colorado, Utah and Wyoming north to southern Montana, and west central Alberta and adjacent British Columbia.

Chorological Affinities.— Few other species of butterflies share the high mountain slopes with *E. magdalena*. Other species of *Erebia* may be found as strays in high mountain habitat, but none are closely related to *E. magdalena*.

Phylogenetic Relationships.— As indicated, *E. mackinleyensis* and *E. magdalena* appear to be sister species. *Erebia magdalena* populations show recognisable differences which can be attributed to subspeciation on isolated mountains. Taxa included are *E. m. magdalena* Strecker and *E. m. saxicola* new subspecies.

Erebia magdalena magdalena Strecker 1880
(Figures 3, 4 - 36, 39 and 43, Tables 1 - 3)

Recognition.— These butterflies are dark brown to black, with individuals in southern populations exhibiting mesial bands (predominantly in females) and occasionally with rust colored scales, but seldom developed as a distinct patch.

Description.—As described for *E. magdalena*.

Geographical Distribution (Figure 58).— *Erebia magdalena magdalena* is known from northern New Mexico, through Colorado, eastern Utah, north to Wyoming and southern Montana.

Chorological Affinities.— Few other high elevation butterflies are found in the same habitat. Some of these are *Oeneis melissa* (*O. m. lucilla* Barnes and McDunnough, in Colorado *O. m. beani* Elwes, in Montana and Wyoming). Other high elevation species are found in adjacent habitats of moist meadows such as *O. polixenes* (Fabricius), *O. taygete* Geyer and *Colias nastes streckeri* Grüm-Grschimailo. No other species of *Erebia* shares the high mountain habitat with *E. magdalena*.

Phylogenetic Relationships.— The very local isolated populations scattered over many mountains has facilatated population differentiation. The analysis of the different populations shows a clinal type relationship (Graphs A and B), with individual character states showing no clear trends. The greatest shift is shown with the Alberta population, described below as a separate subspecies.

Material Examined.—

Adults (males, females). U.S.A.: Colorado; Boulder County; Arapahoe Pass 1, 0 (USNM). Arapahoe Pass Trail 3, 0 (YOUN). Boulder 3, 2 (USNM). Mount Audubon 11, 3 (ALME, AMNH, CNC, USNM). Mount Navajo, ridge east of, 1, 2 (ALME, USNM). Navajo Peak, 1, 0 (USNM). Needles Eye Tunnel, Corona Pass 1, 2 (ALME, SHEP). Niwot Ridge, near Ward 1, 0 (CNC). Clear Creek County; Loveland Pass 40, 11 (ALME, INHS). Mount Kelso 0, 2 (PIKE, YOUN). Custer County; Hermit Pass 1, 0 (PRES). Grand County; Berthoud Pass 2, 0 (YOUN). Corona Pass 2, 0 (ALME). Wheeler Basin 0, 2 (YOUN). Gilpin County; Corona Pass 4, 0 (ALME, AMNH, PRES). Gunnison County; Copper Lake, above 1, 0 (USNM). Cumberland Pass 2, 0 (SHEP). East Maroon Pass 9, 1 (SPER). Yule Pass 0, 1 (SPER). Hinsdale County; Mount Umcompadre 0, 1 (SPER). La Plata County; Chicago Basin 1, 0 (AMNH). Larimer County; (Rocky Mountain National Park) 6, 3 (ALME, CNC, USNM). Longs Peak 3, 1 (ALME, AMNH). Peacock Lake 1, 1 (ALME). Specimen Mountain 2, 2 (ALME, USNM). Park County; 2, 0

(USNM). Hall Valley 9, 9 (ALME, USNM). Hoosier Pass 0, 1 (AMNH). Bullion Peak 1, 0 (USNM). Pennsylvania Mountain 0, 1 (ALME). Storm Peak 1, 0 (ALME). Montana: Carbon County; Beartooth Plateau 5, 3 (SHEP). New Mexico: Taos County; Wheeler Peak 4, 3 (INHS). Utah: 3, 0 (ALME, UASM). Summit and Duchesne Counties; Bald Mountain 8, 1 (ALME, PRES). Summit County; 1, 0 (ALME). Uintah County; Leidy Peak 8, 3 (ALME). Wyoming: Fremont County; 1, 0 (USNM).

Immatures. U.S.A.: Colorado: Boulder County; Corona Pass, Eggs 3 (shells), 1st instar 1 (UASM). Grand County; 1st instar 1, 4th instar 1, 4–5th instar (died in moult) 1, 5th instar 1, photographs of larvae and pupa (YOUN).

Erebia magdalena saxicola, NEW SUBSPECIES
(Figures 1, 2, 4, 5, 8 - 33 and 41, Tables 1 - 3)

Derivation Of Subspecific Epithet — The subspecies is named for its association with rocky habitat. All specimens were captured on a boulder field on top of a mountain. *Saxicola* from Latin means 'inhabits rocks'.

Type Material.— Holotype: male, Adams Lookout, Alberta Forestry Service, Wilmore Wilderness Park, Alberta, 1.viii.81, G.J. HILCHIE. Allotype: 24.vii.81, same locality data.

Paratypes: 27 males, 19 females, Adams Lookout, AFS, Wilmore Wilderness Park, Alberta, 4.vii.81, K. AVERY; 1.viii.81, G.J. HILCHIE; 11.vii.82, F.A.H. SPERLING; 12.vii.82, F.A.H. SPERLING; 12.vii.82, E.M. PIKE; 13.vii.82, E.M. PIKE; 24.vii.82, G.J. HILCHIE; 25.vii.82, G.J. HILCHIE; 29.vii.84, G.J. HILCHIE; Mount Hamell, 23.vii.84, K. AVERY; 25.vii.84, K. AVERY; 30.vii.84, K. AVERY; 26.vii.85, G.J. HILCHIE; 27.vii.85, G.J. HILCHIE; 28,vii.85, G. HILCHIE; Dore River, near McBride, British Columbia, 15.viii.84, D. L. THREATFUL.

Type material is deposited in the following institutions: holotype, allotype, and 6 paratypes, CNC; 4 paratypes, USNM; 6 paratypes, UASM; 5 paratypes, Alberta Provincial Museum, Edmonton; 8 paratypes, AVER; 10 paratypes, HILC; 5 paratypes, SPER; 2 paratypes, PIKE. 2 paratypes, SHEP.

Type Locality.— Adams Lookout, Alberta Forestry Service, Wilmore Wilderness Park, 43 km southeast of Grande Cache, Alberta, Canada.

Recognition.—This subspecies is distinguished from *Erebia magdalena magdalena* by the following features: males have scattered white hairs on the ventral surface of the wings; females have scattered white scales and hairs on the ventral surface of the wings (Figures 1, 2 and 4) with concentrations near the apex of the forewing, mesial wing bands absent; geographic range confined to Alberta and B.C.

Description.—

Adults (Figures 4, 31–33 and 41). Male: wings with ground color, dorsal and ventral dark brown to black without pattern, androconial scales present; forewing length 23.8 ± 1.2 mm[1], range 21.4–26.1 mm; hind wing length 19.9 ± 0.9 mm, range 17.7–21.7 mm, n=28; ventral surface of wings with scattered white hairs near apex of forewing and on central area of hind wing (Figure 2). Genitalia typical for *E. magdalena* as illustrated in Warren (1936, Plate 35, Figure 327 and 330). Claspers various in shape (Figures 32 and 33). Gnathos, uncus and aedeagus typical for *E. magdalena* (Figure 31).

Haploid chromosome number is 29 (mode number from counts).

Female: wings with color similar to male; forewing length 25.0 ± 1.4 mm, range 22.1–27.7 mm; hindwing length 20.5 ± 1.3 mm, range 17.2–22.8 mm, n=20; ventral surface of wings with white hairs near tip of forewing and on most of hindwing (Figure 1). Twelve of 16 females examined had from a few to hundreds of white or very pale scales near the tip of the forewing and on the central area and margins of the hindwing. Four females appeared to have their wings dusted with white scales when viewed at low magnification.

Immatures (Figures 5–30). As figured and previously described.

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[1]One standard deviation

Habitat.— *Erebia magdalena saxicola* inhabits alpine boulder fields (ca. 2200 to 3000 m), interspersed with patches of vegetation (Figure 6).

Geographic Distribution (Figure 58).— Known from Adams Lookout, (Wilmore Wilderness Park) and Mount Hamell in Alberta and in an adjacent area in British Columbia which are widely disjunct from the next nearest known populations, found in southern Montana.

Chorological Affinities .— *Erebia discoidalis* Butler, *E. epipsodea* Butler, and *E. disa* Thunberg overlap in range with *E. m. saxicola* None of these species share the high mountain habitat.

Phylogenetic Relationships.— *Erebia magdalena saxicola* is the sister group of *Erebia magdalena magdalena*.

Material Examined.— Type material only.

LIFE CYCLE AND BEHAVIOUR OF *EREBIA MAGDALENA SAXICOLA*

Behaviour of Adults

Males and females (about 1:1) are in the same flight area from July 4 to August 1. They fly over areas of rocks covered with the black lichens *Hypogymnia oroarctica* Krog., *Umbilicaria proboscidea* (L.) Schrad., *U. hyperborea* (Ach.) Hoffm., *Pseudephebe pubescens* (L.) Choisy, and the yellow crustose lichen *Rhizocarpon geographicum* (L.) DC. Rock areas are interspersed with patches of vegetation in the centers of polygon frost formations (Figure 6). Vegetation is high mountain alpine, with the ground cover dominated by *Dryas hookeriana* Juz., *Salix arctica* Pall. and *Silene acaulis* L. Other plant taxa are *Saxifraga oppositifolia* (L.), *Oxitropis podocarpa* A. Gray, *Cassiope tetragona* (L.), *Carex* spp. and various alpine grasses, *Festuca saximontana* Rydb. and *Poa alpina* (L.) (Porsild, 1974).

Erebia magdalena saxicola adults fly in association with many alpine butterfly species but only a few are found in the same habitat [*e.g.*, *Boloria astarte* (Doubleday and Hewitson) and *Oeneis melissa* (Fabricius), see Table 4.]. Some of these species are near the limits of their ranges, *e.g.*, *Boloria napaea alaskensis* (Holland) is at its southern limit and *Boloria alberta* (Edwards) at is at its northern known limit.

Adults fly in sunshine from about 1000 hr to 1730 hr. Females have a wandering flight over the rocks, periodically landing to bask or visit flowers. Males appear more directed in flight, and dark butterflies that pass near them are pursued with great vigor. These included female *E. magdalena*, other males, and males and females of *Oeneis melissa*.

Oviposition

Oviposition in the field occurs in areas of loose rock which are covered by black lichen. One female observed ovipositing backed down the side of a rock (Figure 7) and laid a single egg on the underside near an edge (egg shown on rock in Figure 8). Eggs laid in the field are not placed near plants.

Development

In the laboratory, females laid eggs on any substrate (rocks, cage, water container), preferring sides and lower surfaces. Oviposition normally occurred in the early morning, with some eggs being laid in late afternoon.

Table 4. List of butterflies collected at or near Adams Lookout, Alberta Forest service, Wilmore Wilderness Park, Alberta (1980-1983).

Species	Collection areas				
	Valley	Subalpine	Alpine [1]		
	willows, meadows	pine, fir, spruce	wet meadows	dry meadows	rocks, scree
Erynnis persius Scudder	++[2]				
Hesperia comma manitoba Scudder	+++	++			
Pyrgus centaurae freija Warren	++	+			+
Carterocephalus palaemon mandan Edw.	++				
Euchloe creusa Dbld.	+				
E. ausonides ausonides Lucas	+				
Anthocharis sara Lucas [3a]	+				
Colias meadii elis Strecker		+	+		
C. alexandra christina Edw.	+++	+			
C. nastes streckeri Gr. Gr.			+	+++	+
C. pelidne minisini Bean	+				
C. philodice philodice Godart	++				
C. interior interior Scudder	+				
Pieris napi oleracea Harris	+	+			
P. protodice occidentalis Reak.			+	++	+
Parnassius phoebus Fabricus [3a,b]		+++	++		
Papilio machaon L.	+				+
P. machaon X *zelicaon*					++
P. zelicaon Lucas	+				+
P. glaucus canadensis R. & J.	++	+			
Plebjus argyrognomon scudderii Edw.	++	+			
P. saepiolus amica Edw.	++				
P. aquilo megalo McD.	+	+	+	+	
Glausopsyche lygdamus Dbld.	+++	+			
Everes amyntula Boisduval	++				
Celastrina argiolus lucia Kby.	+	+			+
Lycaena phleas arethusa Dod.	+++	+	+	+	
L. cupreus snowi Edw.	+	+		+	
L. dorcas Kby.	++	+			
L. mariposa Reakirt	+				
Erebia disa mancinus Dbld.	+				
E. epipsodea epipsodea Butler	+++	+			
E. magdalena saxicola n.ssp.					+++

(continued on next page)

Table 4 (continued)

Species	**Collection areas**				
	Valley	Subalpine	Alpine [1]		
	willows, meadows	pine, fir, spruce	wet meadows	dry meadows	rocks, scree
Oeneis c. chryxus Dbld.	++	+++	+		
O. melissa beanii Elwes				+	+++
O. polixenes brucei Edw.				++	
O. taygete edwardsi dos Passos			+	+	
O. jutta chermocki Wyatt		+			
Boloria napaea alaskensis Holland				+++	+
Boloria epithore Edw. [3a]		+			
B. eunomia nichollae Barnes & Benjamin			+		
E. eunomia dawsoni B. & McD.	+++	++			
B. frigga saga Staudinger		+	+	+	
B. improba youngi Holland				++	
B. alberta Edw.					+
B. a. astarte Dbld.				+	++
B. titania grandis B. & McD.		+++	+		
B. freija freija Thunberg		+	+		
Speyeria mormonia eurynome Edw.		+	+	++	+
Phyciodes c. campestris Behr		++			
Euphydryas editha beani Skinner				+	
E. anicia anicia Dbld.		+++		+	
Nymphalis milberti Lat.	+	+	+	+	+
N. antiopa L.		+			
Vanessa cardui L.					+
Polygonia faunus rustica Edwards		+			

1. Some species collected are migrants from lower elevations "hill topping".
2. Key to symbols: + uncommon (1-3 specimens); ++ common (4-10 specimens); +++ abundant (11+ specimens) Numbers are based on specimens collected during visits to the alpine habitat.
3. Additional species from nearby mountains: 3a. Horn Ridge; 3b. Mount Hamell).

Table 5. Rates of development for immatures of *Erebia magdalena saxicola*.

Stadia	Development Time (days/stadia)		Sample Size
	Minimum	Maximum	
egg	11	12	110[1]
first	4	6	75
second	8	36	31
third	14	68	18
fourth	22	90	11
fifth	99[2]	-	1
pupa	7	-	1

[1]. Numbers refer only to those individuals which matured and moulted to the next stadium.

[2]. Includes time while in diapause in an incubator (33 days below +4°C)

Larvae were reared in the laboratory. Development from egg to adult required a minimum of 165 days. Eggs and early instar larvae were maintained at 20–23°C. Development was rapid and mortality high. Table 5 summarizes rates of development

Fourth, and especially fifth instar larvae were slower in development than the first 3 instars. The surviving fifth instar larva pupated after a 99 day stadium including 63 days at 20–25°C and 33 days at +4 to -2°C. During cold treatment larvae were provided with food. One larva continued to feed at +4°C for a few days. Upon removal from the incubator fifth instar larvae were given fresh food. The larvae did not resume feeding (T=20°C, photo period natural short day). Larvae were returned to the incubator for five days at +4°C then brought out in another attempt to stimulate feeding. The temperature was raised to 25°C and they were placed under artificial photoperiod of 16 hours of light and 8 hours of dark. All larvae resumed feeding. Of the 11 reared to fifth instar and brought through the incubation process, 10 contracted a fungal infection and died, one pupated and emerged as an adult. In the molt from fifth instar to pupa, the head capsule splits (Figure 9) and is shed posteriorly with the rest of the larval cuticle. Pupal period at 25°C had a duration of 7 days (n=1) and a female emerged.

By comparison with the natural time span available for development with the rate of development in Table 5, I infer that larvae falcultatively overwinter in Alberta as second or third instar larvae with potential for diapause in any larval instar. Rates of development barring diapause are sufficient that the species should normally complete one generation per year, but two or three years may be required pending unfavourable climatic conditions.

Food Plants.— Larvae were fed grasses throughout rearing. First instar larvae were given a choice of black lichen, fleabane, willow, dandeleon, larkspur, lawngrass clippings, and barley. Larvae readily ate grass clippings and barley. The lawn clippings were a mixture of creeping fescue and Kentucky blue grass. Judging from the oviposition site and non-specificity of food grasses, larvae will eat most grasses of the alpine zone.

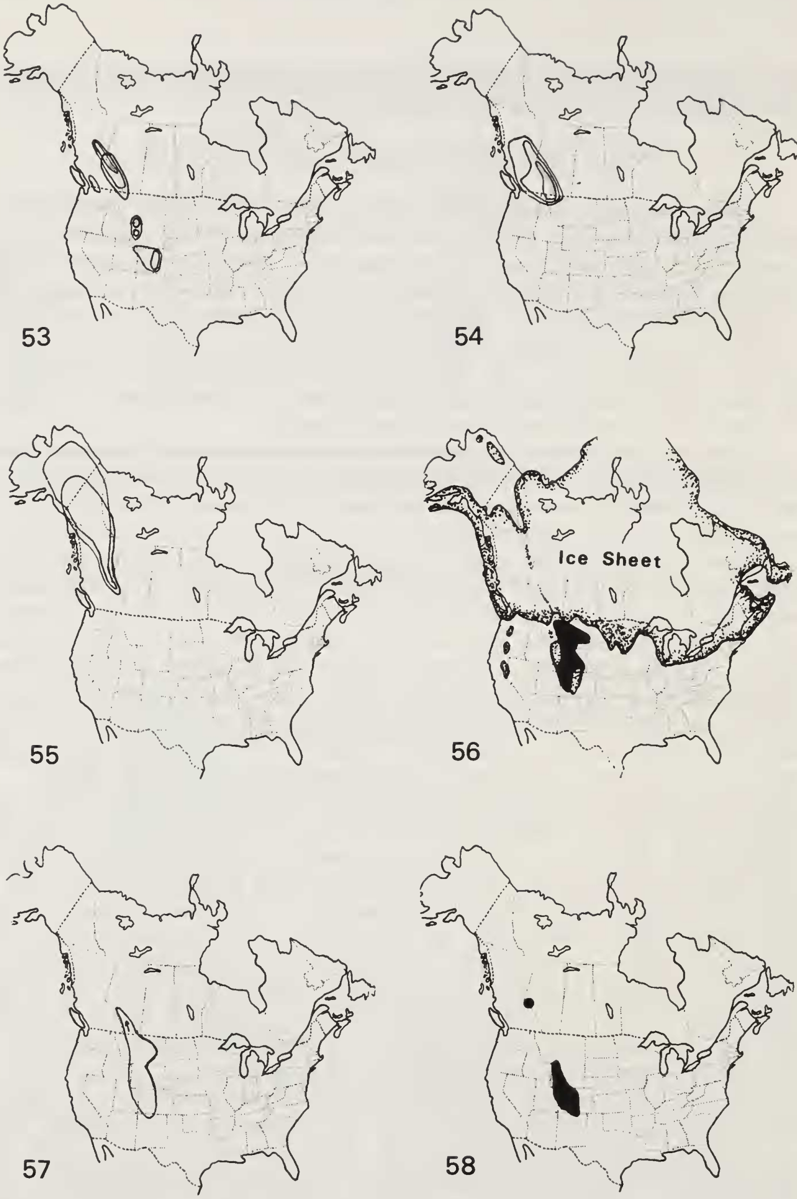
EVOLUTION OF *EREBIA MAGDALENA* STRECKER

Erebia magdalena belongs to a group of Rocky Mountain arctic-alpine butterflies the components of which are distributed more or less discontinuously from Colorado to Alaska. *Erebia magdalena* is the southern sister-species of the Beringian *Erebia mackinleyensis*. This pair of vicars is likely the descendant of an ancestral arctic-alpine stock the range of which was interrupted by one of the pre-Wisconsinan glaciations, since it is unlikely that the surviving stocks would have differentiated to the species level in the time interval embraced by the Wisconsinan glacial stage plus the Holocene (See Whitehead, 1972:334-337, for a discussion of rates of speciation in insects).

Erebia magdalena/mackinleyensis stock dispersed into North America from Asia during one of the early glacials. Subsequent dispersal and isolation during glacial and interstadial periods caused speciation of *Erebia magdalena* and *Erebia mackinleyensis*.

Time of differentiation within *Erebia magdalena* could be comparatively recent, for the included taxa are very similar to one another. Two hypotheses have been proposed that would account for both the discontinuity in range between the two subspecies and their differentiation. Scudder (1979) proposed that the Alberta fauna has a southern affinity and dispersed northward from Wisconsinan-time refugia located south of the ice as the glacial ice melted and exposed the underlying soil. Subsequently, as the climate became more temperate, alpine stocks moved upward to suitable sites at higher altitude on the slopes of the Rockies, with consequent interruption of geographical ranges.
On the other hand, Pike (1980) proposed that various arctic-alpine stocks of butterflies of southern affinity survived the Wisconsinan glaciation on known nunataks and thus were isolated for an extended period of time from their counterparts which survived in suitable habitats south, or north of the ice. As a result of isolation, differentiation took place, at least to the subspecies level (see Kavanaugh (1979:39-40)), for discussion of rates of subspeciation in montane carabids). Although the geological evidence favoring existence of nunataks on the eastern slopes of the Rockies seems firm, and a few plants (Packer and Vitt 1974) exhibit distribution patterns consistent with survival in such areas (also proposed by Pike 1980, for two butterfly subspecies), I am not convinced that nunataks did serve as refugia for butterflies.

I have re-examined distribution data for alpine butterflies (Ferris and Brown 1980; Shepard, British Columbia butterfly distribution maps, pers. comm.; Bird *et. al.*, Alberta butterfly distribution maps, pers. com.; Ferris *et.al.*, 1983). Of the 12 taxa examined by Pike (1980), four are not restricted to above treeline (*E. editha beani*, *L. phleas arethusa*, *L. cupreus snowi*, and *B. e. nichollae*). The remaining eight may be considered true alpine/tundra insects. Mapping generalized ranges for each recognizable subspecies, six are distributed widely in the Alberta and British Columbia Rockies with some populations also in the Canadian coastal ranges and in the Rocky Mountain states of the United States (Figures 53 and 54), implying a refugium south of the ice. Two other species show a northern origin (Figure 55) with a distribution pattern extending along the mountains (personal collecting records show *B. improba* at several localities including, Alberta— Adams Lookout, Horn Ridge, British Columbia— Torrens River, Thunder Mountain and Pink Mountain) from the Yukon. This



Figures 53-58. Butterfly distribution and proposed Pleistocene scenerio maps. Fig. 53. Generalized distribution for *Oeneis polixenes brucei*, *O. taygete edwardsii*, and *O. melissa beani*. Fig. 54. Generalized distribution for *Colias nastes streckeri*, *Boloria astarte astarte*, and *B. alberta*. Fig. 55. Generalized distribution for *Boloria improba youngi* and *B. napea alaskensis*. Fig. 56. Posible distribution of *Erebia magdalena ca*. 1700 B.P. with continuous range in a Wisconsinan refugium. Fig. 57. Dispersal and movement of *E. magdalena ca*. 1200 B.P. north along the foothill ranges following retreating ice sheets. Fig. 58. Present range of *E. magdalena* following climatic readjustments, extinctions and isolation with subspecies differentiation. (dot = *E. m. saxicola*, black area = *E. m. magdalena*).

differs from Pike's proposed interpretation: the range of the one disjunct (*B. improba*), actually extends along the mountains and the one supposed endemic (*B. eunomia*) is not actually a true alpine species but has a wide ranging lowland form, surrounding the highland form that occurs in the Mountain Park area (Cadomin, Alberta).

In terms of available biogeographic data there is no firm support of the hypothesis that a few butterfly species survived on nunataks in northwestern Alberta between the ice sheets. All the alpine butterfly species found in Alberta have portions of their ranges in unglaciated areas south or north of the limits of the Wisconsinan Ice sheet.

If the character states of a population are intermediate between populations found in Alaska and Colorado, it would be reasonable to assume that this population is a relict of a former cline and may have moved to its present location from a nearby refugum. If character states of a geographically intermediate population are not intermediate between those of the geographically adjacent populations, but closely related to one of the populations it would then be more reasonable to assume that these populations share a common parental stock. Present distributions are the result of local extinctions, and migrations over time, creating the illusion of long distance dispersal. It would appear more parsimonious to propose that even for those taxa which show subspecific differentiation, and are not intermediates of a cline, that their parental stocks dispersed from refugia along the northern or southern margins of the ice sheet, and that their differentiation in Alberta is post-glacial in age. I believe this is true of *Erebia magdalena*, and the following scenario including the history of *Erebia mackinleyensis* is based on this belief.

At the zenith of the Wisconsinan Glacial stage the parent stock of *Erebia magdalena* is postulated to have occupied alpine-tundra habitat south of the ice in areas of Montana, Wyoming and Colorado (Figure 56). During melting of the ice mass, the butterflies followed newly developing habitat north along the Rocky Mountain foothills, probably in an ice free corridor (Prest 1969) (Figure 57). Dispersal rate would be affected by dispersal rate of host grasses. Continued climatic amelioration caused suitable lowland habitats to disappear, forcing populations up the east slopes of the Rockies. Isolation of butterfly populations occurred at this time (circa 10,000 years BP).

As the climate continued to ameloriate, alpine-tundra habitats were displaced higher up the mountains. Aridity in the alpine zone of southern Alberta and Montana may have led to shifts in floral composition resulting in local population extinctions of certain butterfly species possibly due to chinook conditions resulting in dry mild winters with very little protective snow cover. The vicariance of *Erebia magdalena* populations (Figure 58) is thus postulated. Three alpine butterfly species, *Oeneis polixenes brucei*, *Oeneis melissa beani*.and *Oeneis taygete edwardsii* have a similar vicariance with populations in the north (Alberta Rockies) and south (southern Montana, Wyoming and Colorado, Figure 53).

Isolation of relatively small populations of *Erebia magdalena* in the northern Rockies created conditions conducive for genetic drift, resulting in subspecfic differentiation.

CONCLUDING STATEMENT

Erebia magdalena is in the process of speciation, although isolation and speciation did not occur during, but after the Wisconsinan glacial and continues